Cattle exclosure and vegetation dynamics in an ancient Irish wet oakwood

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Cattle exclosure and vegetation dynamics in an ancient, Irish wet oakwood

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Abstract The effects of a 10-year period of cattle exclosure on the ground flora and tree regeneration of an Irish ancient lowland wet oakwood (*Corylo-Fraxinetum deschampsietosum*) community are assessed. The approach was to record changes in a quadrat sample located in a National Nature Reserve and to model change by multivariate statistical analysis using Principal Components Analysis and Redundancy Analysis ordination. Exclosure gave significant increases in the abundance of regenerating ash *Fraxinus excelsior* and holly *Ilex aquifolium*. Non-native tree species establishment also occurred. In the ground flora, there were significant decreases in the abundance of ruderal species and grasses and significant increases in graze-resistant and graze-sensitive species usually restricted to broadleaf woodland habitats. Changes were similar under low and high canopy sites, but greater under a high canopy. In Irish lowland wet oakwood, managed historically to favour oak and currently grazed by cattle, exclosure promotes the succession of ash to the canopy and holly to the understorey. With time, this is likely to lead to a shift from oak dominance. In a conservation context this, together with an increased risk of non-native tree species establishment, can be ecologically damaging, particularly in small sites without natural dynamics, as is the case in the hedged agricultural landscapes of western Europe. We conclude that site-based conservation objectives should be prioritised when implementing generic, landscape-scale management strategies, such as rotational exclosure.

Keywords Conservation · Covariable analysis · Functional groups · Grazing indicator species · Non-native · Principal components analysis · Redundancy analysis

Abbreviations

PCA	Principal components analysis
RDA	Redundancy analysis
TWINSPAN	Two-way indicator species analysis

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Introduction

European broadleaf woodlands have a long history of anthropogenic disturbance and management (Mitchell 1995; Rackham 1996). Their structure is simpler than more natural, old-growth forests in other parts of the world (Peterken 1996) which are characterised by a multi-layered canopy, well-developed understorey and complex tree age-structure. Seminatural broadleaf woodlands in cultural landscapes are more usually restricted to isolated patches. In Ireland, upland woods are often unenclosed and grazed by sheep, but lowland woods on farms are generally

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enclosed in a hedged landscape and are often grazed by cattle (Cooper et al. 1997; McEvoy et al. 2006).

Corney et al. (2004) showed that at a landscape-scale, British broadleaf deciduous woodland is structured primarily by geographic, climatic and soil variables (in particular rainfall, soil pH and accumulated temperature) and secondarily by the biotic variables of sheep grazing and leaf area index (an indicator of shading). At a site-scale, management activities are of major importance. Peterken (1993), for example, describes how heavy grazing and trampling by large herbivores such as deer, cattle and sheep can damage lowland broadleaf woodland. The effects include a reduced species diversity of the ground flora, eradication of species from the shrub layer and lack of tree regeneration, mainly by the competitive exclusion of graze-intolerant species (Putman et al. 1989; Mitchell and Kirby 1990; Kelly 2002).

When grazing pressure is reduced or when grazing animals are excluded from woods, graze-intolerant species of the ground flora and shrub layer can recover and there is competitive release of graze-resistant species (Latham and Blackstock 1998; Miles and Kinnaird 1979; Pigott 1983; Putman et al. 1989). The main changes initially are that tree regeneration from seed occurs and that there is an increase in species diversity (Putman et al. 1989; Mitchell and Kirby 1990). Vigorous competition from grasses, forbs and shrubs subsequently reduces species diversity (Kelly 2000; Mitchell and Kirby 1990; Putman et al. 1989). Studies of English seminatural woods have also shown that competition from the ground vegetation can be so great as to prevent further regeneration of some tree species (Linhart and Whelan 1980; Pigott 1983).

Intermediate grazing pressures have been observed to lead to an increased number of species; giving rise to the proposal that rotational exclosure will promote species diversity in cultural ecosystems lacking natural dynamics (Mitchell and Kirby 1990). Little is known about the effects of low and intermediate grazing intensities on woodland plant communities, particularly in lowland situations where, in contrast to upland woods, mesotrophic herbaceous species with woodland habitat preferences are much more frequent.

In Ireland, with its oceanic climate and generally wet soils, studies into the effects of grazing on lowland woods have been few (McEvoy et al. 2006; Perrin et al. 2006, 2008). We assess the effects of cattle exclosure on the ground flora and the tree regeneration of an ancient western Irish wet oakwood National Nature Reserve. We also assess the influence of canopy structure, by comparing the changes between a high canopy site and a low canopy site (the result of past timber extraction). Our article considers the implications for conservation management in the context of the biogeographically isolated nature of Ireland, with its relatively impoverished flora compared with other parts of Europe (Webb et al. 1996), and the close proximity of non-native, introduced tree species seed sources introduced (Lister and Foster 1992).

Study sites

The sites studied are the Reilly and Gole Woods in County Fermanagh, located in the National Trust Crom estate in the north-western Ireland (Fig. 1). They are designated as a National Nature Reserve under the Nature Conservation and Amenity Lands (Northern Ireland) Order 1985. The woods are situated on adjacent low elevation (50–60 m) drumlins (low rounded hills of glacial deposits) on the shores of Upper Lough Erne. The soil is mainly a heavy clay of high base status and impeded drainage. On this soil, both woods are dominated by *Quercus petraea*, *Fraxinus excelsior*, *Corylus avellana*, *Betula pubescens* and *Ilex aquifolium*. In the ground flora, *Deschampsia caespitosa*, *Oxalis acetosella*, *Carex sylvatica* and *Hedera helix* are abundant. *Circaea lutetiana* and *Brachypodium sylvaticum* are frequent, and there is a high frequency of bryophytes, in particular *Eurhynchium striatum*, *Eurhynchium praelongum* and *Rhytidiadelphus triquetrus* (Gordon et al. 1984).

Both woods are considered to be ancient (at least pre-1719), with a history of grazing and periodic timber extraction (Lister and Foster 1992). Some timber extraction took place across both woods during 1910–1914. Felling also occurred in Gole Wood during 1939–1945 and again in 1951–1956, when it was clear-felled except at the outer margin. This wood has a lower canopy (c10 m) compared with Reilly Wood (>20 m). When designated as a National Nature Reserve, the woods were fenced to exclude farm stock. Prior to exclosure, grazing was by cattle for periods in the summer. While there are

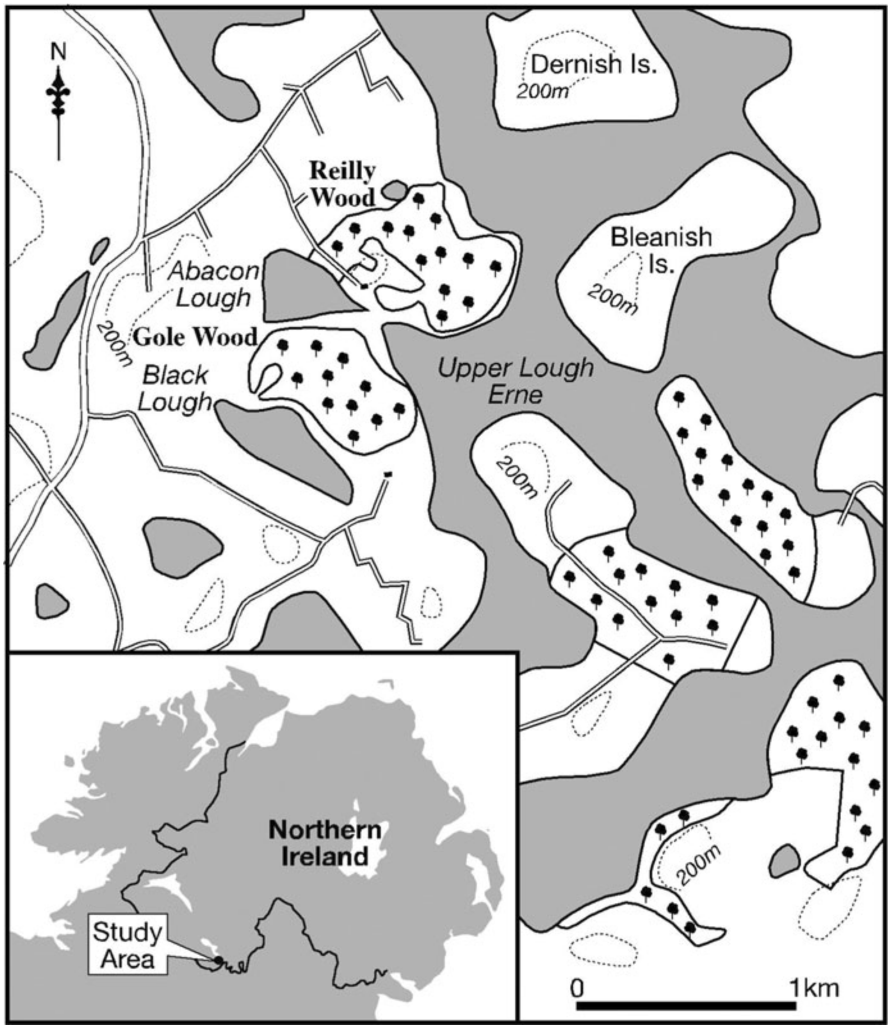

Fig. 1 The location of the Reilly and Gole Wood National Nature Reserve

no records of stock numbers, grazing was known to be of low intensity.

Methods

In 1983, the Reilly and Gole Woods were surveyed with a standardised field procedure (Bunce and Shaw 1973) to establish the species composition of the ground flora (Gordon et al. 1984). Fifty eight permanently marked square quadrats 200 m^2 were sampled from points located on a 100-m grid. In each quadrat, all the species of vascular plants <1.3 m high were recorded, and an assessment of the percentage ground cover of each species was made. Plant species cover in each quadrat was assessed visually by a method shown by Brakenhielm and Qinghong (1995) to perform well in comparison with objective quantitative measures.

A hierarchical, divisive, two-way indicator species analysis (TWINSPAN) classification (Hill 1994) of the baseline quadrats (Gordon et al. 1984) was carried out to guide a resurvey sampling programme. Quadrats from the main TWINSPAN group, comprising more than 50% of the baseline quadrats, were resurveyed. Key TWINSPAN indicator species of the group were *Carex sylvatica* and *Deschampsia caespitosa*. Unsampled quadrats from the remaining TWINSPAN groups represented the woodland vegetation of lower elevation peaty gleys.

Re-survey field work was carried out in July 1996 (corresponding to the baseline seasonal survey date) using the same methods as for the baseline study. A random set of 10 quadrats from Reilly Wood and 11 from Gole Wood were sampled. Plots were relocated using numbered permanent grid-posts erected at baseline and by measuring from the known points using a baseline quadrat distribution map. Field records were made independently of the baseline survey data sheets. One of the authors took part in the baseline survey and the re-survey. Following completion of the re-survey, two quadrats were selected from each wood and comparison with the baseline field data sheets was made in the field to assure that changes in the species were not identification artefacts. The following species could not be separated taxonomically: *Geum urbanum/rivale* (most specimens were clearly *Geum urbanum*), *Quercus petraea/robur* (most specimens were fairly typical of *Q. petraea*) and *Salix* spp. (most specimens were *S. cinerea*). Nomenclature follows Stace (1991). Bryophytes were not recorded at resurvey.

An exploratory Detrended Correspondance Analysis ordination (ter Braak and Smilauer 1998) indicated that a linear species/environment response model was appropriate for multivariate analysis, and therefore, the samples were analysed by Principal Components Analysis (PCA) to assess gradient structure. Species occurring in <3 of the 42 sample quadrats were omitted from the ordination analysis to reduce any distorting effects. A square-root transformation was carried out to reduce the influence of species with high variance and the ordination was species centred. In order to clarify ordination diagrams, only species occurring more than 10 times in the dataset were plotted.

The autecology of Irish species (Webb et al. 1996), mean-weighted Ellenberg indicator values for light, water and nitrogen (Hill et al. 1999; Ellenberg 1979) and mean-weighted life history traits for stress tolerance, competition and disturbance (Grime 1979; Hodgson et al. 1995) were used to assess change. Mean-weighted values were calculated for each quadrat and plotted passively on the PCA ordinations (i.e. as supplementary variables) to guide informal interpretation. Time and site were also plotted passively as nominal variables representing the effects of resurvey and Gole Wood, respectively.

Redundancy analysis (RDA) ordination was carried out to formally assess patterns of variation in the species data that could be explained by time and site (ter Braak and Smilauer 1998). The hypothesis of non-significant deviation of variation explained by a variable, from that explained by a random variable, was tested with the Monte Carlo permutation method in CANOCO 4.5 (ter Braak and Smilauer 1998) with 99 unrestricted permutations of the constraining variable. Significance was tested at the $P = 0.05$ level. In order to determine which species in each site showed significant changes in abundance between baseline and resurvey, *t*-values of the correlation coefficient between species abundance and time on an RDA with the effects of site partialed out by covariable analysis were calculated.

Results

The total number of species at baseline in the sample quadrats from the two woods was similar, and the mean number of species per quadrat was not significantly different between woods (Table 1). Species with a high frequency and cover values were the same in both woods. Species with the greatest abundance in both woods at baseline were *Carex sylvatica*, *Deschampsia caespitosa*, *Oxalis acetosella* and *Rubus fruticosus*. In Reilly Wood, there was more *Agrostis stolonifera*, *Dryopteris filix-mas*, *Luzula sylvatica* and *Primula vulgaris,* and in Gole Wood, there was more *Carex sylvatica*, *Deschampsia caespitosa* and *Geum urbanum/rivale*. The frequency of the tree species *Corylus avellana*, *Fraxinus excelsior*, *Ilex aquifolium* and *Quercus petraea/robur* in the ground flora, was high in both woods. The similarity of species composition and abundance was reflected in the small eigenvalue for the first axis of a DCA ordination (Table 2), indicating that all the key species were present across the main gradient of species composition.

The first two axes of the PCA ordination accounted for 27% of the sample variation (Table 2). The first axis separated Gole quadrats from Reilly quadrats (Fig. 2), showing that quantitative differences in species composition between sites was the greatest source of variation. The Gole quadrats and species such as *Geum urbanum/rivale*, *Carex sylvatica* and *Deschampsia cespitosa*, with habitat preferences for heavy clay soils (Webb et al. 1996) were correlated negatively with the first axis (Fig. 3). The Reilly quadrats and species such as *Luzula sylvatica*, *Vaccinium myrtillus* and *Quercus petraea/robur*, indicative of better-drained, more acidic soils were correlated positively with the first axis.

Table 1 Ground flora percentage frequency (*F*) and cover (*C*) in the baseline quadrat sample

Species	Reilly		Gole	
	F	*C*	*F*	*C*
Agrostis capillaris	90	(2.5)	55	(3.9)
Agrostis stolonifera	100	(7.2)	64	(2.6)
Athyrium filix-femina	90	(1.3)	91	(0.9)
Brachypodium sylvaticum	100	(1.8)	82	(3.9)
Carex remota	100	(4.9)	82	(2.4)
Carex sylvatica	100	(3.8)	100	(9.2)
Circaea lutetiana	100	(3.1)	91	(3.6)
Corylus avellana	90	(0.9)	64	(0.6)
Deschampsia caespitosa	100	(4.4)	100	(19.6)
Dryopteris dilatata	80	(1.0)	91	(0.2)
Dryopteris filix-mas	100	(0.4)	18	(0.3)
Fragaria vesca	80	(1.6)	82	(0.8)
Fraxinus excelsior	100	(1.0)	100	(1.4)
Geranium robertianum	90	(3.5)	82	(2.6)
Geum urbanum/rivale	80	(0.8)	91	(5.0)
Hedera helix	100	(3.6)	100	(4.4)
Ilex aquifolium	90	(0.9)	100	(1.4)
Lonicera periclymenum	90	(2.9)	100	(4.4)
Luzula sylvatica	80	(4.8)	45	(2.1)
Oxalis acetosella	90	(9.0)	91	(5.6)
Potentilla sterilis	90	(1.3)	73	(1.1)
Primula vulgaris	90	(1.3)	55	(0.6)
Quercus petraea/robur	70	(0.7)	82	(0.8)
Rubus fruticosus	100	(3.4)	100	(6.0)
Veronica chamaedrys	100	(1.0)	91	(1.3)
Viburnum opulus	70	(0.7)	45	(0.5)
Viola riviniana	100	(3.4)	100	(2.8)
Total number of species	79	–	73	–
Mean number of species	32	–	35	–

Only species with a frequency >70% in either Reilly or Gole are shown

Table 2 PCA and RDA ordination model parameters

PCA				
Axis	1	2	3	4
Eigenvalue	0.150	0.121	0.111	0.065
Cumulative percentage variance	15.0	27.2	38.3	44.8
RDA				
Axis	1	2	3	4
Eigenvalue	0.102	0.095	–	–
Cumulative percentage variance	10.2	19.7	–	–

The second axis separated baseline quadrats from resurvey quadrats. The baseline quadrats were correlated with high mean-weighted ruderal life history values (*sensu* Grime 1979) and high mean-weighted Ellenberg light indicator values (Ellenberg 1979), suggesting greater disturbance and a more open habitat at baseline (Fig. 4). Separation with time was the greatest in Reilly Wood, showing that community change with time was greater than in Gole Wood.

The first two axes of the RDA direct ordination accounted for 20% of the sample variation (Table 2). This represents a large proportion (72%) of the variation accounted for by the indirect PCA, showing that the variables site and time in the RDA explained most of the variation in species composition accounted for by the PCA. Site and time were both significant (at the level $P = 0.05$) explanatory variables in the RDA. The main change in species composition was a reduction in the abundance of grasses (Table 3). Species shown by the RDA to have a significantly reduced abundance with time in both woods (Table 3) were *Agrostis stolonifera* and *Potentilla sterilis*. In Reilly Wood, species with a significantly reduced abundance with time were *Agrostis capillaris*, *Chrysosplenium oppositifolium*, *Dryopteris filix-mas*, *Oxalis acetosella* and *Primula vulgaris* In Gole Wood, species with a significantly reduced abundance with time were *Dactylis glomerata*, *Polypodium vulgare* and *Pteridium aquilinum*.

Species with a significantly increased abundance with time in both woods were seedlings and saplings of *Fraxinus excelsior* and *Ilex aquifolium*. There was also an increased abundance of the graze-resistant species *Luzula sylvatica*, *Carex sylvatica*, *Rubus fruticosus* and *Lonicera periclymenum,* and the graze-intolerant species *Circaea lutetiana*, *Anemone nemorosa*, *Geum urbanum/rivale* and *Ranunculus auricomis*, shade-tolerant species usually restricted to broadleaf woodland habitats (Webb et al. 1996). Species, with a significantly increased abundance in Reilly Wood, were *Circaea lutetiana* and *Rubus fruticosus*. In Gole Wood, species with a significantly increased abundance were *Anemone nemorosa*, *Anthoxanthum odoratum*, *Blechnum spicant*, *Ranunculus auricomis* and seedlings/saplings of *Corylus avellana*. The RDA showed that in Reilly Wood, species generally had larger correlation coefficients with time, indicating their greater changed abundance values compared with Gole.

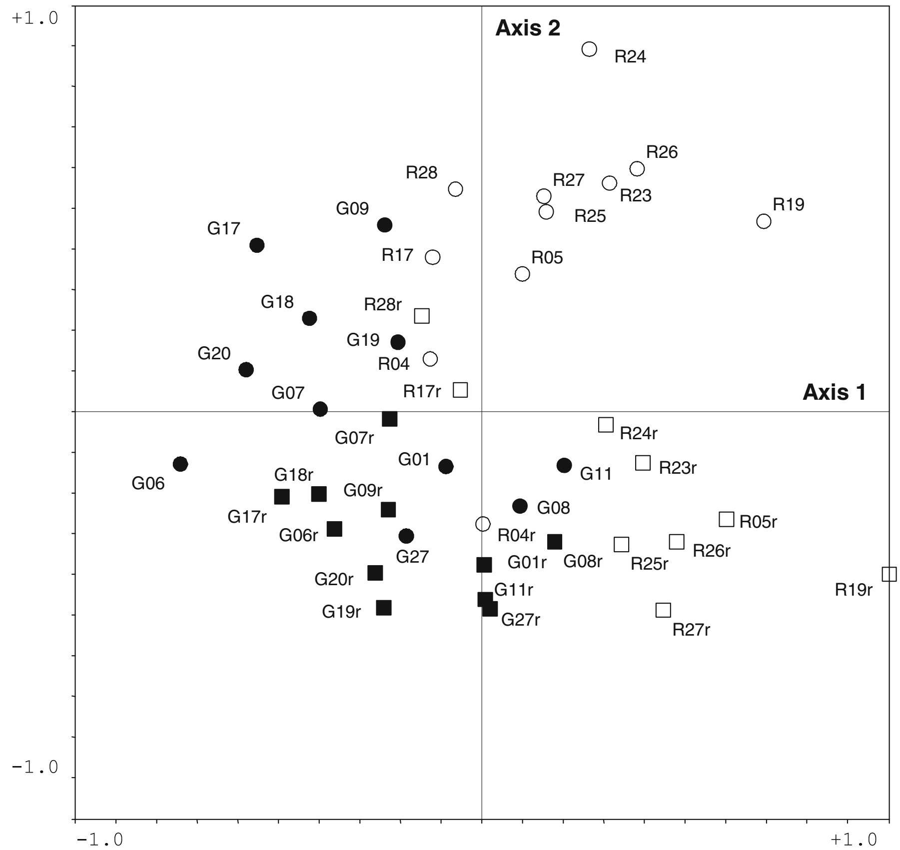

Fig. 2 Sample quadrat Principal Components Analysis ordination. *R* Reilly Wood (*unfilled symbols*), *G* Gole Wood (*filled symbols*), *r* resurvey (*square symbols*), baseline (*circular symbols*)

There was a significant decrease in the mean number of species per quadrat with time in the Gole Wood samples (Table 3). The species lost from or gained (Table 4) had a low frequency (being recorded just once or twice). There were more species lost than gained. Many of the species lost were ruderals (*sensu* Grime 1979) or species of open habitats, but the species gained were mainly indicative of woodland habitats. *Carex laevigata*, an occasional species in Ireland was lost from the Reilly Wood sample and *Carex strigosa*, a scarce species in Ireland, was gained by Gole Wood. The samples also gained *Acer pseudoplatanus*, *Fagus sylvatica*, and *Rhododendron ponticum*, species introduced to Ireland and becoming increasingly naturalised (Dierschke 1982).

Discussion

The ground flora species composition of the Reilly and Gole quadrat samples corresponds closely with the Irish wet woodland sub-association: *Corylo-Fraxinetum deschampsietosum* (Kelly and Iremonger 1997). This vegetation type has affinities with the typical community W9 *Fraxinus excelsior–Sorbus aucuparia–Mercurialis perennis* woodland of the National Vegetation Classification (NVC) of Great Britain (Rodwell 1991), a community of north-western Britain. The small eigenvalues recorded for the first two axes of the Reilly and Gole DCA ordination highlight the ecological similarity of the quadrat samples from each site, a result of sample selection for community homogeneity based on numerical classification. Differences in mean-weighted Ellenberg indicator values, however, indicated small differences in site wetness and mineral nutrient status.

The driver for change was a release of species from grazing pressure and a changed light environment resulting from canopy and ground flora biomass development with time. The effects of cattle exclosure were a reduced abundance and loss of ruderal species (*sensu* Grime 1979) and species of grassland habitats. There was also an increased abundance of

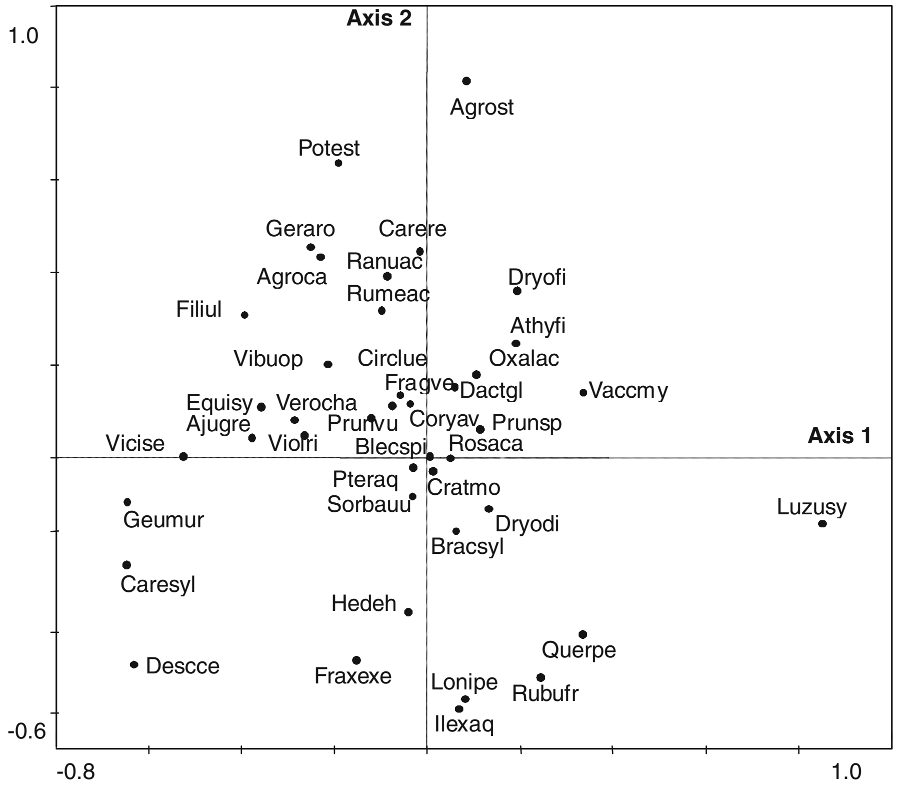

Fig. 3 Principal Components Analysis species ordination. Species occurring in 10 or more quadrats are shown. Species codes: Agroca—*Agrostis capillaris*, Agrost—*Agrostis stolonifera*, Ajugre—*Ajuga reptans*, Athyfi—*Athyrium filix-femina*, Blecsp—*Blechnum spicant*, Bracsy—*Brachypodium sylvaticum*, Carere—*Carex remota*, Caresy—*Carex sylvatica*, Circlu—*Circaea lutetiana*, Coryav—*Corylus avellana*, Cratmo—*Crataegus monogyna*, Dactgl—*Dactylis glomerata*, Descca—*Deschampsia cespitosa*, Dryodi—*Dryopteris dilatata*, Dryofi—*Dryopteris filix-mas*, Equisy—*Equisetum sylvaticum*, Filiul—*Filipendula ulmaria*, Fragve—*Fragaria vesca*, Fraxex—*Fraxinus excelsior,* Geraro—*Geranium robertianum*, Geumur—*Geum urbanum/rivale*, Hedehe—*Hedera helix*, Ilexaq—*Ilex aquifolium*, Lonipe—*Lonicera periclymenum*, Luzusy—*Luzula sylvatica*, Oxalac—*Oxalis acetosella*, Potest—*Potentilla sterilis*, Prunsp—*Prunus spinosa*, Prunvu—*Prunella vulgaris*, Pteraq—*Pteridium aquilinum*, Querpe—*Quercus petraea/robur*, Ranuac—*Ranunculus acris*, Rosaca—*Rosa canina*, Rubufr—*Rubus fruticosus*, Rumeac—*Rumex acetosa*, Sorbau—*Sorbus aucuparia*, Vaccmy—*Vaccinium mrytillus*, Veroch—*Veronica chamaedrys*, Vibuo—*Viburnum opulus*, Vicise–*Vicia sepium*, Violri—*Viola riviniana*

graze-resistant woodland species, seedlings and saplings of ash *Fraxinus excelsior* and holly *Ilex aquifolium* and an increased abundance of graze-sensitive species usually restricted to broadleaf woodland habitats. These changes support the generally accepted view of conservation managers (for which there is little scientific evidence) that the strategy of exclosing agricultural stock is beneficial to the ecological condition of seminatural broadleaf woodland in lowland Britain.

Barkham (1992), in an 18-year study of the ground flora of an ungrazed, formerly coppiced, ancient broadleaf deciduous woodland in Cumbria, encompassing acidic and calcareous soil parent materials, showed that in the absence of canopy management (largely resulting from allowing mixed high forest to develop), it was mainly ruderal and grassland species that were lost. Our study supports these observations by showing that it was mainly light-dependent ruderals that were lost from the Reilly and Gole Woods following exclosure. Barkham (1992) found that shade-tolerant ground flora species were little affected by the absence of canopy management. We show that exclosure was associated with species- and site-specific increases and decreases in the abundance of shade-tolerant woodland species, and those changes were greater under a more developed tree canopy.

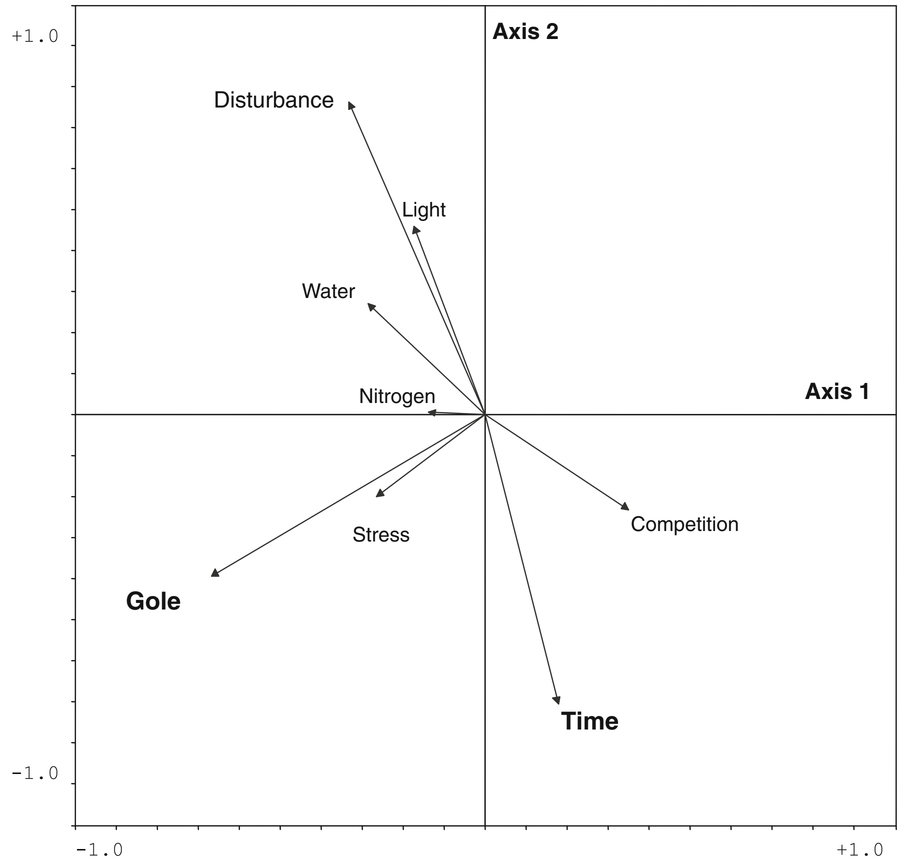

Fig. 4 Indicator variables plotted passively as vectors onto the Principal Components Analysis ordination of samples. Arrow heads represent mean weighted values. Variable codes: Light, Ellenberg light score; Nitrogen, Ellenberg nitrogen score; Water, Ellenberg moisture score. Disturbance, ruderal life history, Competition, competitive life history, Stress, stress life history. The variables Time and Site (Gole) represent the differences between baseline and re-survey and the two woods, Reilly and Gole

Barkham (1992) also showed that species loss and gain from sample quadrats mainly involved statistically infrequent species, and that this was largely a function of sample variability and, therefore, trivial. Similarly, in the Reilly and Gole sample quadrats, the low frequency of species gained and lost, makes ecological inference about these species uncertain. The appearance of the introduced species *Fagus sylvatica*, *Acer psuedoplatanus* and *Rhododendron ponticum*, however, is ecologically significant in terms of a founder population effect, particularly in the context of the National Nature Reserve status of the woods. In contrast to inference based on individual species, the information content of mean-weighted life history strategies (*sensu* Grime 1979) and mean-weighted Ellenberg indicator values (Ellenberg 1979) was informative. The quantitative changes identified by RDA ordination, in which site variation was partitioned out, also provided a clearer model of ecological change than the loss or gain of individual species.

While small, inferred differences in soil wetness and mineral nutrient status between the two woods complicate the interpretation of change, the effects of exclosure were broadly the same in both woods, i.e. decreases in mean-weighted ruderal life history (*sensu* Grime 1979) and Ellenberg light indicator values (Ellenberg 1979). The greater rate of change in community composition in the high canopy Reilly site is related to the development of more densely shading conditions, such as created by the large recorded increase in cover of *Rubus fruticosus*.

The greatly increased abundance of ash *Fraxinus excelsior* and holly *Ilex aquifolium* in the Reilly and Gole Woods was also recorded by Putman et al. (1989) who showed that after 22 years of deer exclusion from lowland broadleaf woodland in the New Forest, England, the vegetation became more homogeneous and relatively species poor, with a shrub layer dominated by *Rubus fruticosus*, *Ilex aquifolium* and *Fraxinus excelsior*. Compared with ash seedlings, oak seedlings have a high requirement

Table 3 Differences in species cover over time

Species	Reilly baseline	Reilly resurvey	Gole baseline	Gole resurvey
Agrostis capillaris	**2.5**	**0.2**	3.9	0.6
Agrostis stolonifera	**7.2**	**2.6**	**2.6**	**0.3**
Anemone nemorosa	0.1	0.5	**0.0**	**0.7**
Anthoxanthum odoratum	0.2	0.2	**0.0**	**0.7**
Blechnum spicant	0.8	0.3	**0.4**	**0.8**
Carex remota	4.9	3.3	2.4	3.2
Carex sylvatica	3.8	4.2	9.2	9.6
Chrysosplenium oppositifolium	**0.4**	**0.0**	0.3	0.5
Circaea lutetiana	**3.1**	**6.5**	3.6	4.2
Corylus avellana	0.9	0.7	**0.6**	**1.0**
Dactylis glomerata	1.2	0.2	**0.6**	**0.1**
Deschampsia caespitosa	4.4	3.9	19.6	12.7
Dryopteris filix-mas	**1.3**	**0.6**	0.6	0.6
Fraxinus excelsior	1.0	3.1	**1.3**	**4.8**
Geum urbanum/rivale	0.8	2.1	5.0	6.6
Ilex aquifolium	**1.0**	**3.8**	**1.4**	**4.8**
Lonicera periclymenum	2.9	4.8	4.4	5.5
Luzula sylvatica	4.8	11.1	2.1	2.9
Oxalis acetosella	**9.0**	**3.4**	5.6	5.9
Polypodium vulgare	0.1	0.0	**0.4**	**0.0**
Potentilla sterilis	**1.3**	**0.0**	**1.1**	**0.0**
Primula vulgaris	**1.3**	**0.5**	0.6	0.6
Pteridium aquilinum	0.3	0.3	**2.1**	**0.0**
Ranunculus auricomis	0.0	0.2	**0.0**	**0.5**
Rubus fruticosus	**3.4**	**18.0**	6.0	8.2
Total species	79	57	73	54
Mean number of species	32	30	35	27

Site-specific significant differences between baseline and resurvey (bold) were determined ($P < 0.05$) from *t*-values of the correlation coefficient between species abundance and time on a reduncancy analysis (RDA) with the effects of site partialled out. Species with a mean percentage cover >4% in any one group and the mean number of species in a group are also shown

for light and a low requirement for nutrients (Dieckmann 1996). Pontailler et al. (1997), for example, showed that for oak seedlings in canopy gaps, mortality in gaps smaller than 100 m^2 attains 95% during the first four years, and 100% during two years in deep shade. Kelly (2002), in an experimental study on the effects of deer exclosure on oak regeneration in the *Blechno-Quercetum* (Braun-Blanquet and Tuxen 1952) of Tomies Wood, over a podzolic soil in south-west Ireland, show that successful oak regeneration is to be expected only in unshaded or lightly shaded sites where grazing intensities are low. This suggests that its contribution to canopy dominance at Reilly and Gole will be much less in the future.

The woodland structure to which the Reilly and Gole sites correspond in Ireland (Kelly and Iremonger 1997) and Britain (Rodwell 1991) is typically dominated by *Fraxinus excelsior* with some *Ulmus glabra*, *Acer pseudoplatanus* and *Quercus petraea*. The large increase in ash *Fraxinus excelsior* and holly *Ilex aquifolium* seedlings and saplings recorded at Reilly and Gole suggests that the proportion of the canopy they will occupy is likely to increase if the woods continue to be unmanaged. Hofmeister et al. (2004) show increased nutrient availability following the reduction of traditional management activities such as coppiced wood removal, litter raking and grazing, probably account for the spread and succession of ash *Fraxinus excelsior* in aging oak-dominated European forests. Our study supports the assertion that cattle exclosure is influential in Ireland. The same conclusion also applies to holly *Ilex aquifolium*.

Table 4 Frequency of species lost and gained from the sample quadrats between baseline and resurvey

Species	Reilly		Gole	
	Losses	Gains	Losses	Gains
Arum maculatum	1			1
Carex laevigata	1			
Lysimachia nemorum	2			2
Luzula pilosa	1		1	
Epilobium montanum	2			
Hypericum pulchrum	2			
Lapsana communis	1			
Listera ovata	1			
Veronica officinalis	1			
Hypericum tetrapterum	1		1	
Holcus lanatus	2			
Juncus bulbosus	1			
Juncus conglomeratus	1			
Lysimachia vulgaris	1			
Taraxacum officinale agg.	1			
Carex panicea	1			
Rumex sanguineus		1		
Orchis mascula		1		
Cardamine flexuosa			1	
Stellaria holostea			1	
Urtica dioica			1	
Cirsium palustre			1	
Galium palustre			1	
Juncus bufonius			1	
Potentilla erecta			1	
Salix sp.			1	
Acer pseudoplatanus				1
Carex strigosa				1
Fagus sylvatica		1		2
Festuca gigantica				2
Rhododendron ponticum		1		
Total species lost or gained	16	4	10	6

Rackham (1995) reviewed the historical ecology of Irish ancient woodland and presented documentary historical evidence suggesting that in ancient woodlands, oak *Quercus* spp. was widely promoted in the past. Service (2002) cites historically documented evidence of oak *Quercus petraea* being the favoured silviculturally in ancient woodlands on the Crom estate at least during the 19th century. This is further indirect evidence that changed tree population size-structures resulting from the exclosure of the Reilly and Gole Woods are likely to lead to the loss of oak *Quercus petraea* dominance, as mature individuals of *Quercus petraea* senesce. A consequence of this is a reduced population of purple hairstreak butterfly *Neozephyrus quercus* (L.), a rare Irish oak canopy species, currently found in the Reilly and Gole Woods. These effects are important in the context of the isolated nature of the Reilly and Gole Woods, their high conservation value and the biogeographic isolation of the Irish flora. Perrin et al. (2006) assessed the effects of long-term deer exclusion on regeneration and stand dynamics in a yew wood and an oak wood in southwest Ireland, and similarly found changed tree regeneration patterns influencing canopy structure.

The potential establishment of non-native tree species into ancient woodland in Ireland is a conservation management issue to which our results contribute. Such establishment in Irish woodland, following disturbance, was demonstrated by Smith et al. (2003) in an experimental study of clear-felled upland Sitka spruce plantations. They showed that the most abundant species regenerating naturally were the non-native *Abies alba*, *Fagus sylvatica*, *Larix kaempferi*, *Picea sitchensis*, *Pinus contorta*, *Pinus sylvestris* and *Rhododendron ponticum*. In a survey of Irish seminatural woodland, Perrin et al. (2008) described high frequencies of *Acer pseudoplatanus*, *Fagus sylvatica* and *Rhododendron ponticum*. The presence of *Fagus sylvatica*, *Acer pseudoplatanus* and *Rhododendron ponticum* in the Reilly and Gole resurvey samples highlights the potential of disturbance to facilitate the establishment of founder populations. The detrimental effect of the introduced species on Irish woods is exemplified by the widespread occurrence and dominance of *Rhododendron ponticum* in the *Blechno-Quercetum* (Braun-Blanquet and Tuxen 1952) native Irish oakwoods of Killarney (Cross 1975). The introduced *Acer pseudoplatanus* is widespread in Irish seminatural woodland, and while detrimental ecological effects have not been categorically demonstrated (Peterken 2001), its establishment in the Reilly and Gole National Nature Reserve is likely to be seen as contributing to a decrease in ecological condition.

Conservation management recommendations to maintain species diversity in grazed upland woodlands proposed by Mitchell and Kirby (1990), are introducing a partial reduction in grazing for periods, grazing at low or moderate levels and implementing rotational exclosure. The rationale is to maintain heterogeneity in cultural ecosystems which lack natural dynamics. Our study shows that conservation management by site exclosure was initially beneficial to the ecological condition of the woodland sites, allowing graze-sensitive, shade-tolerant woodland species to recover from grazing and trampling. We thus concur with observations by Mitchell and Kirby (1990) about initial biodiversity gains from exclosure and show that they will also occur across different canopy structures. We agree that management by rotational exclosure can have ecological benefits, given the long-term detrimental effects of heavy grazing or permanent exclosure, but suggest that, in Irish conservation sites, the development of founder populations of non-native species associated with recovery from heavy grazing disturbance, should be the focus of conservation action. More generally, we conclude that site-based conservation objectives should be prioritised when implementing generic, landscape-scale management strategies, such as rotational exclosure proposed by Mitchell and Kirby (1990).

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